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Research article

Effects of shade on agronomic traits of doubled haploid lines of eggplant (*Solanum melongena* L.) obtained from anther culture

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Abstract: Low-light stress can inhibit plant growth and production. The selection of superior genotypes that are adaptive and tolerant to low light intensity needs to be performed. This study evaluated the agronomic responses of ten doubled haploid lines of eggplant and three varieties to various shade levels (0%, 25%, and 50%). This study used a split-plot design with three replicates. The results indicate that 25% shade is the optimal selection environment for shade tolerance. Genotypes grown under 25% shade exhibited varying responses, with two genotypes classified as shade-loving, seven as tolerant, three as moderately tolerant, and one as shade-sensitive. Shade levels of up to 50% significantly reduced yield, with production dropping to 58%–81% of the unshaded conditions. In general, growth characteristics such as plant height, leaf width, and leaf area were better under shaded conditions, whereas the yield was better under unshaded conditions. AM 23, AM 14, and AM 10 showed better tolerance responses and maintained better yields than the other lines under 25% shade. This study provides important insights into the development of shade-tolerant eggplant varieties. These findings can be used as a basis for recommendations for eggplant planting in shaded areas such as agroforestry systems.

Keywords: anther culture; doubled haploid; eggplant; light; photosynthesis; shade tolerance

1. Introduction

Eggplant, also known as brinjal *(Solanum melongena* L), is an important vegetable widely cultivated globally. Eggplants are cultivated in tropical and subtropical countries [1,2]. Eggplant belongs to the Solanaceae family and is a close relative of potatoes, chili peppers, and tomatoes. Eggplant ranks 10th as a vegetable, with a high content of phenolic compounds and antioxidants [3]. The demand for eggplants continues to increase with the increasing global population. The increasing demand for eggplants is accompanied by decreased agricultural land area. Globally, eggplant land area has fluctuated over the last five years, from 2019 to 2022 [4]. In addition, agricultural land ownership per person in 2021 amounted to 0.2 hectares, a decrease of 18 percent over the past 21 years [5].

In Indonesia, the harvest area for eggplant has decreased by 133 ha from 50,533 ha in 2021 to 50,400 ha in 2022 [6]. The number of farming households with land ownership of less than 0.5 ha still accounts for 58% of the total number of farming households. This makes it important to increase the efficiency of agricultural land use [7].

Agroforestry systems and intercropping of forestry, plantations, and yard crops can be a solution to increase land-use efficiency in Indonesia. However, low light intensity can disrupt the plant metabolic processes. Light is indispensable for photosynthesis, a complex biochemical and biophysical process in biomass production that involves photosynthetic pigment synthesis, the Calvin cycle, and light-controlled electron transport [8]. Shade can limit photosynthesis and indirectly affect carbon gain potential through morphological and physiological acclimatization responses [9–11].

Eggplant is a C3 crop that can grow under low light intensities [12]. At shade levels up to 25%, eggplants usually responded well. Previous studies have shown that eggplant plants exhibit good tolerance under 21% shade [13]. In other Solanaceae species, shading tolerance varies, with chili plants tolerating up to 25% shade [14] and tomato plants up to 50% [15] when using shade-tolerant genotypes. Additionally, a recent study found that cayenne pepper produced higher yields under 50% shade compared to unshaded conditions [16]. This has led to the importance of using shade-tolerant crop varieties with high yields. The utilization of land under stands requires the use of varieties that can grow, develop, and produce well under shade stress [17].

Eggplant breeding programs mostly focus on developing hybrid varieties because of the large effect of heterosis on eggplant productivity [2, 18]. The development of hybrid varieties requires pure lines with high homozygosity as crossing parents [19,20]. Conventional breeding methods using recurrent selection have high costs and a long time of 6–10 generations [21]. An alternative method to quickly obtain pure lines is through anther culture techniques. The process involves producing haploids from hybrids through anther, pollen, or ovule culture, doubling the chromosomes, and resulting in stable and fertile plants [22]. Doubled haploid (DH) lines hold potential in plant breeding and genetics due to their speed and efficiency in obtaining complete homozygosity compared with conventional inbred lines [23]. The time required to produce doubled haploid plants through anther culture techniques is much faster than what conventional methods require [24,25]. Anther cultures can obtain pure lines in only one generation [26–29]. The resulting doubled haploid plants can be directly evaluated and selected as new hybrid parents [25]. Doubled haploid plants can be selected directly as inbred varieties. Doubled haploid technology has been widely utilized to enhance stress tolerance in various crop species. Doubled haploid lines have been evaluated in maize under drought stress [30], camelina under two irrigation conditions [31], flint maize under cold stress [23], and wheat under salinity stress [32]. However, studies on stress tolerance in doubled haploid eggplant remain limited.

Research on the selection of environments related to shade tolerance is essential for an effective and efficient eggplant variety breeding program. However, information related to this is limited. The growth and production of eggplant lines at each shade level must be evaluated. Previous studies have obtained eggplant doubled haploid lines [25], which should be further tested under shade conditions to determine their tolerance and adaptation to shade stress. This study aimed to determine the differences in agronomic characteristics of eggplant doubled haploid lines in response to different level of paranet shading.

2. Materials and methods

2.1. Experimental design

This study was conducted at the Pasir Kuda Experimental Farm of the PKHT IPB, Bogor, West Java, between January and May 2024. The experiment was arranged in a split-plot design, with two factors and three replicates. The first factor in the main plot was shade application, namely 0%, 25%, and 50% shade. The second factor included 10 doubled haploid lines and three varieties as subplots. Eggplant-doubled haploid lines were selected based on good agronomic characteristics [33]. The experiment consisted of three replicates with a total of 117 experimental units, each consisting of four plants. The genotypes used in this study are listed in Table 1.

Table 1. Genetic material of 14 eggplant genotypes.

No.	Genotype	Description	No.	Genotype	Description
1	AM4 (P)	Doubled haploid	8	AM14 (M)	Doubled haploid
2	AM6 (P)	Doubled haploid	9	AM23 (P)	Doubled haploid
3	AM8 (H)	Doubled haploid	10	AM28 (P)	Doubled haploid
4	AM9 (H)	Doubled haploid	11	Hitavi F1	Commercial variety
5	AM10 (H)	Doubled haploid	12	Provita F1	Commercial variety
6	AM11 (H)	Doubled haploid	13	Mustang F1	Commercial variety
7	AM13 (M)	Doubled haploid			

The letters in parentheses represent the codes indicating the parent's name: (P) = Provita F1, (H) = Hitavi F1, (M) = Mustang F1.

2.2. Experiment procedure

Seeds were sown in nursery trays placed in a greenhouse with a medium of husk charcoal, soil, and manure in a ratio of 1:1:1. Each genotype was sown in 36 seeds per seedling tray. Watering was performed at least once a day. Tillage was performed four weeks before transplanting, including soil plowing and harrowing, bed formation, manure application, and basic fertilization. Each bed was given 20 kg of cow manure and 0.5 kg of lime. The basic fertilizers used were urea (200 kg ha^{-1}), SP-36 (150 kg ha^{-1}), and KCl (150 kg ha^{-1}), which were given one week before planting. Silver-black plastic mulch was installed on each bed, and planting holes with a diameter of 10 cm were made using a dibble with a planting distance of 0.5 m x 0.7 m.

The shade was created by installing a paranet with shade densities of 0%, 25%, and 50% on all sides of the shade frame. Shade construction was performed two weeks before planting. The frame was made of bamboo, with an installation direction from east to west, to obtain maximum sunlight. The height of the paranet was 3 m. Transplanting was performed when the eggplant seedlings were four weeks after sowing and had 3–4 leaves. Planting was performed in the afternoon to prevent the seedlings from wilting due to sunlight. Each eggplant seedling was planted in one planting hole and then watered with sufficient water, followed by installing a stake. Replanting was performed if the plants died within two weeks after planting (2 WAP).

Maintenance activities included watering, replanting, fertilizing, pinching, pest control, and disease control. Fertilization was performed using NPK 16-16-16 at a concentration of 10 g L^{-1} and a dose of 250 mL per plant by dripping it into each plant hole. Pinching was performed when the water buds were present below the first branch of the main stem. Weeding was performed manually by pulling weeds around the plants. Pest and disease control was performed if symptoms of pest and disease attacks occurred. Pesticides were applied at the recommended dosages.

Harvesting was performed according to the harvest criteria. The criteria for harvesting eggplant fruit were that the flesh was not yet hard, the color of the fruit was shiny, the size was not too large or small, golden yellow seeds were not visible when cut, and the color of the flesh was pure white. Harvesting was performed gradually up to 12 times. The characters observed in this experiment were agronomic characters consisting of plant height (cm), crown width (cm), dichotomous height (cm), stem diameter (cm), leaf length (cm), leaf width (cm), leaf area (cm^2), days to flowering (DAP), days to harvesting (DAP), fruit weight (g), number of fruits, fruit weight per plant (g), fruit length (cm), fruit diameter (cm), weight per bed (g), and productivity (tons ha^{-1}). Observations of the microclimate components consisted of light intensity (lux), daily temperature (°C), and relative humidity (%). Daily temperature and relative humidity were measured using a USB temperature and humidity data logger.

2.3. Data analysis

The observed data were analyzed using *analysis of variance (*ANOVA). If in the variance analysis there was a significant effect at the 5% real level, then the differences between treatments were further tested with honestly significant difference (HSD) using the Statistical Tool for Agricultural Research (STAR) version: 2.0.1 and R-Studio software version: 4.4.1. The plant tolerance level grouping was determined based on the relative production of plants [15]. Based on this, eggplant genotypes were grouped according to the following criteria: (1) sensitive genotype if relative production is <60%, (2) moderate genotype if relative production is 60–80%, (3) tolerant genotype if relative production is 80–100%, and (4) shade-loving genotype if relative production is >100%. Pearson correlations were conducted using RStudio (R-Studio 4.4.1).

3. Results and discussion

3.1. Effects of shade on the microclimate of the experimental environment

Shading is a method for maintaining the productivity and quality of vegetable crops [13]—providing shade changes the microclimate. In this experiment, observations were made of the microclimate, namely, light intensity (Lux), temperature (°C), and humidity (%). Average light intensity ranged from 50.659 lux to 99.099 lux, daily temperature ranged from 31.24 °C to 34.39 °C, and humidity ranged from 76.72 to 80.92% (Table 2). The shade net-linked microclimate observations showed clear trends. When comparing 25% and 50% with unshaded conditions, there was a decrease in light intensity of 24.46% and 48.88%, respectively. Likewise, a decrease in temperature at 25% and 50% shading was 5.21% and 9.16%, respectively, compared to that under unshaded conditions.

Table 2. Microclimate under 0%, 25%, and 50% shade.

Variables	Shade		
	0	25%	50%
Light Intensity (Lux)	99099	74861	50659
Daily Temperature (°C)	34.39	32.60	31.24
Humidity (%)	76.72	79.23	80.91

The humidity under 25% and 50% shading increased between 3.27% and 5.46%, respectively. Higher shading reduces light intensity, increasing humidity and lowering temperatures, which affect photosynthesis. Reduced light intensity reduces the amount of photosynthetically active radiation (PAR), which can interfere with plant growth. Intercropping can reduce light intensity by 10–80% [34]. Based on previous research, eggplants can still produce well at 21% shade during the fall period [13].

Table 3. Analysis of variance of 13 eggplant genotypes under 0%, 25%, and 50% shade.

Characters	Shade (E)	Genotype (E)	G×E	CV
Plant height	5.719^{ns}	3.3187 **	0.3437^{ns}	17.89^{t}
Crown width	1971.27*	209.6**	31.8^{ns}	16.04
Dichotomous height	489.69**	117.72**	4.34^{ns}	10.74
Stem diameter	0.0081^{ns}	0.0327**	0.0025^{ns}	7.3t
Leaf length	1094.19**	113.27**	7.07^{ns}	2.76
Leaf width	206.986**	19.435**	1.058^{ns}	11.67
Leaf area	150669**	20865**	1809^{ns}	9.77
Days to flowering	15.41^{ns}	108.942**	8.123^{ns}	16.09
Days to harvesting	0.9703*	0.0648**	0.0165**	8.96t
Weight per fruit	0.4609^{ns}	103.5404**	0.9415^{ns}	11.6t
Fruit length	0.84^{ns}	983.26**	2.76*	7.43
Fruit diameter	0.0157^{ns}	0.0555**	0.0359**	8.47^{t}
Number of fruits per plant	1.7613*	0.6627**	0.0201**	16.68^{t}
Fruit weight per plant	27.805**	0.7405**	0.0927^{ns}	18.16^{t}
Weight per bed	56.3349**	1.5044**	0.1894^{ns}	18.37^{t}
Productivity	3.9525**	0.1038**	0.0167^{ns}	15.66^{t}

CV = Coefficient of variance, * = significant effect at α = 5%, ** = significant effect at α = 1%, ns = not significant effect at α = 5%, t = transformed data = ($\sqrt{x + 0.5}$).

Analysis of variance showed that genotype, shade, and interaction factors significantly affected the observed characters (Table 3). Genotypes significantly affected all the observed characters, indicating genetic variation between the genotypes used in the experiment. The effect of shade significantly affected some of the measured character, indicating appropriate environmental conditions for the experiment. The interaction factor of genotype and environment showed a varied response; in general, it did not significantly affect most of the characters observed except for the characters of harvest age, fruit length, fruit diameter, and number of fruits per plant. The difference in responses to the interaction of genotypes and environment indicates that shade provides different responses to genotypes in each environment. In this experiment, genotype contributed the most to all observed characters compared to shade and its interaction. This indicates that the different responses to eggplant yield under shaded conditions depend on genetic factors.

3.2. Agronomic character

The variability in morphological and physiological characters is influenced by several factors, including light intensity [35–37] and light period [35]. Shade conditions can increase plant height and chlorophyll content and improve fruit quality, but there is a reduction in plant productivity [38,39]. Plant height is an important factor that affects fruit set and color [40]. As shown in Table 4, genotype had a significant effect on plant height, but there was no significant effect of shade or interaction, indicating that the genotype showed similar responses to shade treatment. Genotype AM10 was the tallest genotype (89.27 cm), while the shortest was AM6 (60.27 cm). Shade levels and genotype significantly affected dichotomous height; however, there was no significant interaction (Table 4). The 50% shade treatment had the highest dichotomous average (27.21 cm), which was significantly different from that of the 25% shade (23.59 cm) and unshaded conditions (20.12 cm). The reduction in light intensity under shading conditions induces stem elongation, known as the shade avoidance syndrome (SAS), as a response to maximize light capture [41]. This elongation is caused by an uneven distribution of auxin. Auxin plays a key role by enhancing cell sensitivity to elongation through its interaction with phytochrome-interacting factors (PIF) and auxin/indole acetic acid (Aux/IAA) [42].

Genotypes significantly affected stem diameter, but there was no significant effect of shade or its interaction (Table 4). Genotype AM13, Mustang F1 (1.44 cm), had the largest stem diameter, followed by Hitavi F1 (1.39 cm), and with the smallest stem diameter genotype AM23 (1.07 cm). Reduced stem diameter under shaded conditions is attributed to biomass allocation in response to light availability. The decrease in stem diameter may be caused by a decrease in endogenous zeatin concentration [43]. Zeatin is an active cytokinin-type plant hormone that regulates growth and promotes cell division [44]. A smaller stem diameter under shaded conditions can also be caused by changes in lignin content, such that the stem becomes more slender, weak, and unstable [45].

Leaves are important organs for carbon capture under shade stress conditions [46]. The shade level and genotype significantly affected leaf length, but there was no significant interaction (Table 5). The 50% shade treatment resulted in the longest average leaf length (31.21 cm), which was significantly different from that of the 25% shade (25.37 cm) and unshaded (20.63 cm) treatments. AM10 (30.72 cm) had the longest leaves, followed by AM8 (29.13 cm), and the shortest leaf genotype AM28 (20.42 cm). The shade level and genotype significantly affected leaf width, but there was no significant interaction (Table 5). The 50% shade treatment resulted in the widest average leaf (13.25 cm), which was significantly different from that of the 25% shade (10.71 cm) and unshaded (8.65 cm) treatments. The genotype with the widest average leaf was Hitavi F1 (12.99 cm), followed by AM8 (12.76 cm), which was significantly different from the genotype with the smallest leaf width, AM28 (8.80 cm). Plants experiencing stress due to prolonged shading undergo morphological and physiological changes as a mechanism of shade avoidance syndrome (SAS). The shade-avoidance response results in changes in leaf morphology that maximize light capture [47]. Another change caused by shading is a decrease in leaf thickness, damage to chloroplast structure, and a reduction in the chlorophyll a/b ratio, which can disrupt plant photosynthesis [48].

Table 4. Means of plant height, dichotomous height, and stem diameter as influenced by shades or eggplant genotypes.

Treatment	Plant height (cm)	Dichotomous height (cm)	Stem diameter (cm)
Shade			
0%	67.08	20.12^{C}	1.30
25%	76.50	23.59^{B}	1.22
50%	79.55	27.21^{A}	1.27
Genotype			
AM4 (P)	66.08^{cde}	20.18^{de}	1.13^{c}
AM6 (P)	60.27^{e}	20.09^{de}	1.11^{c}
AM8 (H)	84.06^{a}	24.48^{bcd}	1.46^{a}
AM9 (H)	65.86^{de}	20.75^{cde}	1.10^{c}
AM10 (H)	89.27^{a}	27.67^{ab}	1.40^{ab}
AM11 (H)	81.88^{ab}	25.19^{abc}	1.24^{abc}
AM13 (M)	79.02^{abc}	26.96^{ab}	1.44^{a}
AM14 (M)	76.21^{abcd}	26.64^{ab}	1.38^{ab}
AM23 (P)	61.10^{e}	17.81^{e}	1.07^{c}
AM28 (P)	62.36^{e}	19.35^{e}	1.04^{c}
Hitavi F1	86.28^{a}	24.57^{abcd}	1.39^{ab}
Mustang F1	84.24^{a}	29.18^{a}	1.44^{ab}
Provita F1	70.28^{bcde}	24.46^{bcd}	1.21^{bc}

Numbers followed by the same lowercase letter (genotype) and uppercase letter (shade) in the same column for each character are not significantly different based on the 5% HSD test.

Shade and genotype significantly affected the leaf area, but there was no significant interaction (Table 5). Fifty-percent shade showed the largest average leaf area (241.15 cm^2), and was significantly different from 25% shade (165.97 cm^2) and unshaded conditions (117.82 cm^2). The genotypes with the largest average leaf area were AM10 (239.52 cm^2), followed by Hitavi F1 (234.56 cm^2), and were significantly different from the genotype with the smallest leaf area, AM28 (119.54 cm^2). Under shaded conditions, plants adapt to energy storage efficiency by increasing their leaf area index (LAI) [49]. Leaves also experienced thinning as caused by thinning of the palisade layer and mesophyll cells [50]. Genotype and shade significantly affected crown width, but there was no interaction between the two factors (Table 5). The average of the shade treatments showed that 50% shade had the widest crown (84.98 cm), which was significantly different from the 25% shade (76.31 cm) and unshaded conditions (70.88 cm). The genotypes that had the widest crowns were Hitavi F1 (83.88 cm) and AM23 (80.95 cm), and were significantly different from the genotype that had the smallest crown width, AM6 (63.85 cm). Under shaded conditions, plants adapt by broadening their leaves to enhance light absorption efficiency. This causes the plant canopy to expand to maximize photosynthesis despite the limited available light.

Table 5. Means of leaf length, leaf width, leaf area, crown width, and days to flowering as influenced by shades or eggplant genotypes.

Treatment	Leaf length (cm)	Leaf width (cm)	Leaf area (cm^2)	Crown width (cm)	Days to flowering (DAP)
Shade					
0%	20.63^{C}	8.65^{C}	117.82^{C}	70.88^{B}	32.9
25%	25.37^{B}	10.71^{B}	165.97^{B}	76.31^{B}	33.6
50%	31.21^{A}	13.25^{A}	241.15^{A}	84.98^{A}	34.2
Genotype					
AM4 (P)	22.63^{de}	9.64^{de}	133.86^{cd}	75.18^{ab}	32.7^{abc}
AM6 (P)	23.17^{cde}	9.68^{de}	141.48^{bcd}	63.85^{b}	33.1^{abc}
AM8 (H)	29.13^{ab}	12.76^{ab}	231.24^{a}	78.48^{a}	37.0^{a}
AM9 (H)	23.21^{cde}	9.66^{de}	128.35^{d}	80.88^{a}	32.8^{abc}
AM10 (H)	30.72^{a}	12.13^{ab}	239.52^{a}	81.10^{a}	35.7^{ab}
AM11 (H)	25.34^{bcd}	12.14^{ab}	187.62^{abc}	77.61^{a}	33.1^{abc}
AM13 (M)	28.61^{ab}	11.58^{abc}	204.50^{a}	75.49^{ab}	37.0^{a}
AM14 (M)	27.61^{abc}	11.10^{bcd}	195.49^{ab}	75.63^{ab}	36.0^{ab}
AM23 (P)	21.67^{de}	9.05^{e}	119.54^{d}	80.95^{a}	25.3^{d}
AM28 (P)	20.42^{e}	8.80^{e}	113.48^{d}	78.78^{a}	28.9^{cd}
Hitavi F1	30.17^{a}	12.99^{a}	234.56^{a}	83.88^{a}	36.0^{ab}
Mustang F1	28.76^{ab}	11.94^{ab}	215.15^{a}	77.61^{a}	36.8^{a}
Provita F1	23.18^{cde}	9.89^{cde}	129.93^{d}	76.60^{a}	31.7^{bc}

Numbers followed by the same lowercase letter (genotype) and uppercase letter (shade) in the same column for each character are not significantly different based on the 5% HSD test.

The ability of plants to adapt to shade by regulating flowering time is an important strategy. Genotypes significantly affected the days to flowering, but there was no significant effect of shade or its interaction (Table 5). AM23 (25.3 DAP) had the shortest time to flowering, followed by AM28 (28.9 DAP), and AM8 (37.0 DAP) had a late flowering time. Shade and genotype significantly affected the days to harvesting, with significant interaction (Table 6). Despite this interaction, all genotypes showed significantly longer harvesting time under 25% and 50% shade conditions than under unshaded conditions. AM4 (43.1 DAP) had the shortest time to harvest, followed by Provita F1 (46.0 DAP), which had the second-fastest harvest time at all shade levels.

Flowering time is influenced by genotype, temperature, and light intensity received daily by plants [15]. Delayed flowering time is caused by the response of the genotype to shade intensity. Shades of higher intensity resulted in weak photosynthesis, photosynthate accumulation, and competition for photosynthetic products. It also causes delayed bud differentiation and reduces inflorescence and the number of flowers [51]. Previous studies that found the effect of shading on flowering time were on *Antirrhinum majus* [52], ornamental plants [53], Swarnaprabha rice [51], and several soybean lines [54,55].

The ANOVA results showed significant differences between shaded and unshaded plants. In this study, the provision of shade at different levels significantly affected yield. The shade and genotype significantly affected the number of fruits per plant, with a significant interaction between them (Table 6). All genotypes had a significantly higher number of fruits under unshaded conditions than under 25% and 50% shade conditions. Provita F1 (20.8) had the highest number of fruits, followed by AM4 (18.4), the second highest at all shade levels. The number of fruits per plant directly influences the fruit weight per plant through the fruit set [16]. The reduction in the number of fruits per plant is caused by several factors, including reduced fruit set, reduced seeds per fruit, and increased flower abortion [56].

Table 6. Means of days to harvesting of eggplant genotypes at different levels of shade.

Genotype	Days to harvesting (days)				Number of fruits per plant			
	0	25%	50%	Mean	0	25%	50%	Mean
AM4 (P)	40.0^{Aa}	40.0^{Ab}	49.3^{Ae}	43.1	26.7^{Aa}	21.3^{Aab}	7.3^{Babc}	18.4
AM6 (P)	40.0^{Ba}	42.3^{Bb}	70.7^{Aabcde}	51.0	16.6^{Aa}	11.6^{Acd}	4.0^{Bcde}	10.7
AM8 (H)	49.3^{Ba}	58.0^{Bab}	87.3^{Aab}	64.9	5.7^{Ab}	4.3^{ABe}	2.0^{Bde}	4.0
AM9 (H)	40.0^{Ba}	44.7^{ABab}	58.0^{Ade}	47.6	22.8^{Aa}	15.7^{Abc}	4.3^{Bbcd}	14.3
AM10 (H)	51.7^{Ba}	54.0^{Bab}	93.7^{Aa}	66.4	4.7^{ABb}	5.4^{Ae}	2.1^{Bde}	4.1
AM11 (H)	47.0^{Ba}	49.3^{Bab}	79.3^{Aabcd}	58.6	4.2^{Ab}	3.4^{ABe}	1.7^{Bde}	3.1
AM13 (M)	42.3^{Ba}	44.7^{Bab}	78.3^{Aabcd}	55.1	4.7^{Ab}	4.4^{Ae}	1.4^{Be}	3.5
AM14 (M)	42.3^{Ba}	47.0^{Bab}	84.0^{Aabc}	57.8	5.0^{Ab}	4.6^{Ae}	1.3^{Be}	3.6
AM23 (P)	40.0^{Ba}	40.0^{Bb}	64.3^{Abcde}	48.1	20.1^{Aab}	21.7^{Aab}	7.0^{Babc}	16.3
AM28 (P)	40.0^{Ba}	40.0^{Bb}	56.3^{Ade}	45.4	24.4^{Aa}	20.8^{Aab}	7.9^{Bab}	17.7
Hitavi F1	44.7^{Ba}	44.7^{Bab}	65.0^{Abcde}	51.4	7.0^{Ab}	6.3^{Ade}	2.7^{Bde}	5.3
Mustang F1	42.3^{Ba}	65.0^{Aa}	58.7^{Acde}	55.3	6.3^{Ab}	5.0^{Ae}	2.0^{Bde}	4.4
Provita F1	40.0^{Ba}	40.0^{Bb}	58.0^{Ade}	46.0	24.5^{Aa}	27.2^{Aa}	10.8^{Ba}	20.8
Mean	43.1	46.9	69.5		13.3	11.7	4.2	

Numbers followed by the same lowercase letter within the same column and the same uppercase letter within the same row are not significantly different based on the HSD test at a 5% level.

The genotype significantly affected fruit length, with a significant interaction (Table 7). Hitavi F1 (26.32 cm) had the longest average fruit length in each shade, followed by AM13 (25.59 cm), which had the second-longest fruit at all shade levels. Shade and genotype significantly affected fruit diameter, with a significant interaction (Table 7). Genotype AM8 (5.61 cm) had the largest fruit diameter, followed by Mustang F1 (5.24 cm), which had the second-largest fruit diameter at all shade levels. Fruit diameter influences the weight per fruit. Under shaded conditions, plants generally show a reduced fruit size due to a lack of carbohydrates during the early reproductive stages [57]. In addition, a reduction in fruit size can also be caused by a lack of light, as plants experience lower sugar accumulation and fewer petioles [58].

Genotypes significantly affected the weight per fruit, but there was no significant effect of shade or its interaction (Table 8). Mustang F1 (174.61 g) had the largest weight per fruit followed by Hitavi F1 (162.88 g), and the smallest weight per fruit was genotype AM9 (36.07 g). External factors have a significant influence on a plant's ability to achieve optimal production. Shading treatment alters the microclimate of the experimental environment, including temperature and humidity, which ultimately affects the amount of light available for photosynthesis [14]. Plants growing under shaded conditions experience a decline in net photosynthetic rate, stomatal conductance, and chlorophyll content. Additionally, damage to chloroplast ultrastructure and the photosynthetic system occurs, ultimately leading to a reduction in yield [59–61]. Additionally, the reduction in fruit weight can also result from a shift in the balance between production and growth mechanisms, where the plant prioritizes growth over yield.

Table 7. Means of fruit diameter and fruit length of eggplant genotypes at different levels of shade.

Genotype	Fruit length (cm)				Fruit diameter (cm)			
	0	25%	50%	Mean	0	25%	50%	Mean
AM4 (P)	5.30^{Bc}	7.38^{Ab}	4.06^{Bd}	5.58	4.38^{Ab}	4.46^{Ab}	4.54^{Aa}	4.46
AM6 (P)	4.07^{Ac}	4.15^{Ab}	5.66^{Ad}	4.63	4.28^{Ab}	4.42^{Ab}	4.40^{Aa}	4.37
AM8 (H)	22.94^{Ab}	24.04^{Aa}	22.95^{Abc}	23.31	4.71^{Bab}	7.60^{Aa}	4.51^{Ba}	5.61
AM9 (H)	5.65^{Ac}	4.27^{Ab}	4.16^{Ad}	4.69	4.32^{Ab}	4.38^{Ab}	4.26^{Aa}	4.32
AM10 (H)	23.69^{Aab}	23.99^{Aa}	23.98^{Abc}	23.89	4.06^{Ab}	4.04^{Ab}	4.54^{Aa}	4.21
AM11 (H)	23.41^{Aab}	23.03^{Aa}	22.29^{Ac}	22.91	4.61^{Aab}	4.63^{Ab}	4.43^{Aa}	4.56
AM13 (M)	24.64^{Bab}	24.04^{Ba}	28.09^{Aa}	25.59	4.81^{Aab}	4.51^{Ab}	4.44^{Aa}	4.58
AM14 (M)	24.88^{Aab}	24.66^{Aa}	26.36^{Aab}	25.30	4.72^{Aab}	4.29^{Ab}	4.36^{Aa}	4.46
AM23 (P)	4.46^{Ac}	4.43^{Ab}	4.59^{Ad}	4.49	4.35^{Ab}	4.37^{Ab}	4.39^{Aa}	4.37
AM28 (P)	4.18^{Ac}	5.28^{Ab}	4.23^{Ad}	4.56	4.34^{Ab}	4.41^{Ab}	4.39^{Aa}	4.38
Hitavi F1	26.55^{Aa}	26.09^{Aa}	26.32^{Aab}	26.32	5.23^{Aab}	4.43^{Ab}	4.53^{Aa}	4.73
Mustang F1	25.52^{Aab}	26.12^{Aa}	26.37^{Aab}	26.00	6.26^{Aa}	4.57^{Bb}	4.90^{Ba}	5.24
Provita F1	4.29^{Ac}	4.26^{Ab}	4.35^{Ad}	4.30	4.40^{Aab}	4.41^{Ab}	4.35^{Aa}	4.39
Mean	15.35	15.52	15.65		4.65	4.66	4.47	

Numbers followed by the same lowercase letter within the same column and the same uppercase letter within the same row are not significantly different based on the HSD test at a 5% level.

Shade and genotype significantly affected the fruit weight per plant; however, there was no significant interaction (Table 8). The fruit weight per plant is influenced by the weight per fruit and the number of fruits per plant. The unshaded conditions showed the highest weight per fruit, with an average weight of 942.07 g, followed by 25% shade (800.00 g), significantly different from 50% shade (257.87 g). The genotype with the largest average fruit weight per plant was Provita F1 (880.28 g), followed by Mustang F1 (877.35 g), and the smallest fruit weight per plant was AM6 (464.43 g). Based on observations, it is evident that the Provita F1, despite having a low individual fruit weight, exhibited the highest total fruit weight per plant. This phenomenon can be attributed to the high number of fruits produced by the Provita F1, which compensates for its lower individual fruit weight, thereby maintaining a high total fruit weight per plant.

Shade and genotypes significantly affected fruit weight per bed, but there was no significant interaction (Table 8). The average fruit weight per bed of the shade treatments showed that unshaded conditions had the highest fruit weight per bed (3768.29 g), followed by 25% shade (3199.99 g), significantly different from 50% shade (1031.49 g). The genotypes that had the highest fruit weight per bed were Provita F1 (3521.10 g), followed by Mustang F1 (3509.40 g), and the smallest fruit weight per bed was genotype AM6 (1857.72 g). Shade and genotypes significantly affected productivity, but there was no significant interaction (Table 8). The average of the shade treatments showed that unshaded conditions had the highest productivity (26.92 tons ha^{-1}), followed by 25% shade (22.86 tons ha^{-1}), significantly different from 50% shade (7.37 tons ha^{-1}). The genotypes that had the highest productivity were Provita F1 (25.15 tons ha^{-1}), followed by Mustang F1 (25.07 tons ha^{-1}), and the lowest productivity was genotype AM6 (13.27 tons ha^{-1}). Plant productivity is influenced by genotype and shade level. Reducing solar radiation beyond 40% under shaded conditions is an important factor that can reduce crop productivity [62]. The difference in plant response to shade is seen in the response curve to *relative sunlight reduction* (RSR); some plants can tolerate a reduction in sunlight, as in fruit crops, berries, and vegetables, and can tolerate up to 30% shade [63].

Table 8. Means of fruit diameter and fruit length as influenced by shades or eggplant genotypes.

Treatment	Weight per fruit (g)	Fruit weight per plant (g)	Fruit weight per bed (g)	Productivity (ton/ha)
Shade				
0%	105.27	942.07[A]	3768.29[A]	26.92[A]
25%	101.40	800.00[A]	3199.99[A]	22.86[A]
50%	101.50	257.87[B]	1031.49[B]	7.37[B]
Genotype				
AM4 (P)	36.25[c]	705.45[ab]	2821.80[abc]	20.16[abc]
AM6 (P)	36.35[c]	464.43[c]	1857.72[c]	13.27[c]
AM8 (H)	152.08[ab]	561.81[bc]	2247.23[c]	16.05[c]
AM9 (H)	36.07[c]	674.73[abc]	2698.92[abc]	19.28[abc]
AM10 (H)	138.04[b]	633.40[abc]	2533.59[abc]	18.10[abc]
AM11 (H)	163.83[ab]	514.83[bc]	2059.32[c]	14.71[c]
AM13 (M)	164.52[a]	640.45[abc]	2561.80[abc]	18.30[abc]
AM14 (M)	159.66[ab]	584.12[bc]	2336.47[bc]	16.69[bc]
AM23 (P)	37.26[c]	643.83[abc]	2575.33[abc]	18.40[abc]
AM28 (P)	36.70[c]	641.66[abc]	2566.64[abc]	18.33[abc]
Hitavi F1	162.88[ab]	844.09[a]	3376.38[ab]	24.12[ab]
Mustang F1	174.61[a]	877.35[a]	3509.40[a]	25.07[a]
Provita F1	37.17[c]	880.28[a]	3521.10[a]	25.15[a]

Numbers followed by the same lowercase letter (genotype) and uppercase letter (shade) in the same column for each character are not significantly different based on the 5% HSD test.

3.3. The yield tolerance levels under 25%, 50%, and unshaded conditions.

Environmental conditions have a significant impact on the productivity of horticultural crops [13]. Based on the results of this study, as presented in Table 9, the results in the unshaded, 25% shade, and 50% shade conditions showed significant differences. The genotypes planted under unshaded conditions yielded better yields than those planted under 25% and 50% shade conditions. Genotypes planted under 25% shade showed higher tolerance to variability responses than those planted under 50%. This result is similar to that of a previous study [64]. High variability can be used to group genotypes into shade-loving, tolerant, moderate, and sensitive categories. The grouping of tolerance levels of the genotypes was based on their relative production. Relative production is the percentage yield in the shade compared to the control. Table 9 shows that while 25% shade increases relative production to more than 100%, production decreases to 82% under 50% shade. These findings are consistent with previous studies reporting that hybrid corn genotypes, which follow the C4 photosynthetic pathway, exhibit increased production under 25% shade but experience a decline at 50% and 75% shade levels [64]. In contrast, cayenne pepper, which utilizes the C3 photosynthetic pathway, shows increased production under 50% shade, with yields surpassing those observed under unshaded conditions [16]. These results indicate that each crop has a distinct response to shading, influenced by its physiological mechanisms. Furthermore, variations in shade response are not solely determined by whether a plant follows the C3 or C4 pathway; even within the same family, species may exhibit different adaptations to shading conditions. Shade-intolerant plants usually exhibit changes in their morphological and physiological characters in response to shade avoidance. Plants that are tolerant of shade usually show only minor physiological and metabolic changes [65].

Table 9. The tolerance level of yield characters of eggplant genotypes to shade.

Genotype	0% (g per plant)	Shade 25% (g per plant)	RP	Category	Shade 50% (g per plant)	RP	Category
AM4 (P)	988.07	874.55	89	tolerant	253.73	26	sensitive
AM6 (P)	687.63	580.77	84	tolerant	124.89	18	sensitive
AM8 (H)	921.65	511.15	55	sensitive	252.62	27	sensitive
AM9 (H)	1011.18	760.32	75	moderate	252.69	25	sensitive
AM10 (H)	860.51	751.92	87	tolerant	287.76	33	sensitive
AM11 (H)	833.47	535.4	64	moderate	175.62	21	sensitive
AM13 (M)	995.6	741.91	75	moderate	183.84	18	sensitive
AM14 (M)	794.65	762.82	96	tolerant	194.88	25	sensitive
AM23 (P)	873.72	800.31	92	tolerant	257.48	29	sensitive
AM28 (P)	889.88	762.22	86	tolerant	272.88	31	sensitive
Hitavi F1	1005.18	1109.14	110	shade-loving	417.97	42	sensitive
Mustang F1	1257.85	1028.63	82	tolerant	345.57	27	sensitive
Provita F1	1127.57	1180.83	105	shade-loving	332.44	29	sensitive

RP: Relative production, AM: Line code.

The yield distribution under different shade levels is visualized in Figure 1 through a boxplot representation. The boxplot indicates that under unshaded conditions (Yield_0), the median yield is the highest, with a relatively narrow interquartile range, reflecting stable production among genotypes. Under 25% shade (Yield_25), the median yield declines, while the interquartile range expands, suggesting increased genotype variability in response to moderate shade conditions. The presence of several outliers indicates that certain genotypes maintain high yields despite shading. In contrast, under 50% shade (Yield_50), the median yield decreases significantly, with a narrower interquartile range and a right-skewed distribution, signifying that most genotypes experience a substantial yield reduction due to increased shade intensity. This pattern indicates that progressively increasing shade levels negatively impact yield, with the highest level of stress observed under 50% shade conditions.

Relative production under 25% shade varied, with hybrid genotypes Hitavi F1 (110%) and Provita F1 (105%) exhibiting higher yields, likely due to improved light interception, photosynthetic rates, or physiological plasticity. In contrast, 50% shade caused a significant yield decline (58%–81%), indicating a critical threshold where shading severely limits productivity. The superior performance of these hybrids under moderate shade may be attributed to hybrid vigor (heterosis), which enhances stress tolerance, photosynthetic efficiency, and metabolic flexibility. Similar findings in maize [66] and chili [67] highlight the role of heterosis in improving shade resilience.

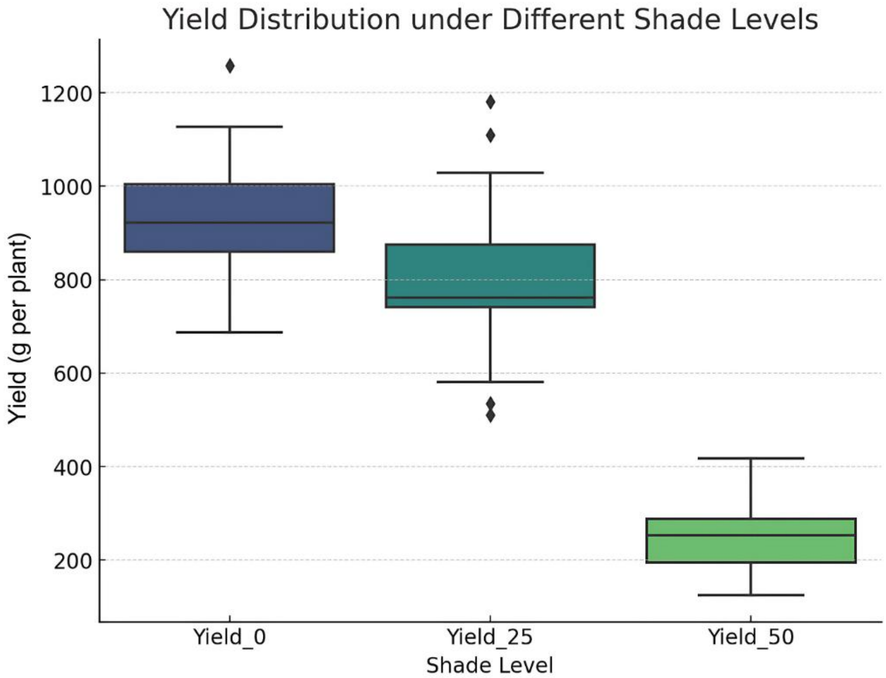

Figure 1. Yield distribution of eggplant (g per plant) under different shade levels.

Based on the level of variability, 25% shade showed higher variability than 50% shade and unshaded conditions, and it was used to determine the shade tolerance. The results of this study differ from those of other C3 plants, like tomato [15,68–70] and chili [71], which showed higher variability under 50% shade conditions compared to 25% shade and unshaded conditions. These findings have significant implications for breeding programs aimed at developing shade-tolerant eggplant varieties. The identification of genotypes with high shade tolerance provides essential selection criteria for enhancing eggplant resilience under low-light conditions. Breeding programs should prioritize the selection of genotypes with superior high yield potential, optimal photosynthetic mechanisms, and morphological plasticity that enable stable productivity in shaded environments. Furthermore, the role of heterosis in improving shade tolerance warrants further investigation through the development of hybrid breeding strategies that integrate genetic traits associated with adaptability to shaded conditions. Given the positive response of hybrid genotypes in this study, breeding programs focusing on appropriate cross combinations have the potential to enhance shade tolerance and yield stability in eggplant production systems. In addition to hybrid development, the shade-tolerant lines identified in this study may also be further developed as inbred varieties.

From a practical perspective, the findings of this study underscore the potential of shade-tolerant eggplant genotypes for intercropping systems, particularly within agroforestry or other shaded environments. The integration of eggplant with companion crops can improve resource use efficiency, particularly in terms of light, water, and soil nutrients, thereby enhancing overall productivity. Additionally, intercropping systems optimize land use and contribute to the sustainability of agricultural production.

The adoption of intercropping systems incorporating shade-tolerant eggplant genotypes presents an alternative strategy for farmers to maximize land utilization and diversify income sources. The inclusion of high-value intercrops can enhance economic returns without necessitating land expansion while simultaneously mitigating the risks associated with monoculture. Furthermore, specific intercrops may contribute to soil fertility improvement and facilitate natural pest control, thereby reducing reliance on synthetic inputs. Consequently, the implementation of intercropping systems in shaded environments, as suggested by these findings, may enhance productivity and economic efficiency while promoting sustainable agricultural practices.

For further validation, future research should focus on identifying the most compatible companion crops for shade-tolerant eggplant genotypes, such as sweet corn or long beans, which can provide partial shading while maintaining optimal growth conditions. The evaluation of these intercropping systems across various climatic regions and soil types will ensure broader adaptability and greater practical relevance for farmers operating in various agricultural settings.

4. Conclusions

Based on the results of this study, 25% shade is a suitable selection environment for low-light stress. Genotypes grown under 25% shade showed various responses to shade stress and we have identified two shade-loving genotypes, Hitavi F1 and Provita F1, seven tolerant genotypes, three moderate genotypes, and one sensitive genotype. Provision of up to 50% shade significantly reduced plant yield, and all genotypes were in the sensitive category. Generally, morphological characters (plant height, dichotomous height, crown width, leaf length, leaf width, and leaf area) were greater under shaded conditions than under unshaded conditions. The flower and yield showed that plants grown under unshaded conditions were better than those grown under 25% and 50% shade conditions. Genotypes AM 23 (Provita F1), AM 14 (Mustang F1), and AM 10 (Hitavi F1) showed responses in the tolerant category, which showed the ability to maintain a better yield than the other lines for each parent in 25% shade. These insights can guide yield improvement under shade stress by targeting traits correlated with fruit weight.

Use of AI tools declaration

The authors declare that they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Author contributions

Samsul Ma'arif: Conceptualization, Methodology, Data curation, Formal analysis, Writing—original draft. Bambang Sapta Purwoko, Arya Widura Ritonga, and Iswari Saraswati Dewi: Conceptualization, Methodology, Supervision, Writing, review and editing.

References

1. Saini DK, Kaushik P (2019) Visiting eggplant from a biotechnological perspective: A review. *Sci Hortic* 253: 327–340. https://doi.org/10.1016/j.scienta.2019.04.042
2. Taher D, Solberg S, Prohens J, et al. (2017) World vegetable center eggplant collection: origin, composition, seed dissemination and utilization in breeding. *Front Plant Sci* 8: 1484. https://doi.org/10.3389/fpls.2017.01484
3. Mahanta CL, Kalita D (2020) Eggplant. In: *Nutritional Composition and Antioxidant Properties of Fruits and Vegetables*, 16 Eds., New York: Academic Press, 273–287. https://doi.org/10.1016/B978-0-12-812780-3.00016-7
4. Food and Agriculture Organization (2024) Food and Agriculture Data.
5. Food and Agriculture Organization (2023) *Land statistics and indicators 2000–2021*, Italy: FAO.
6. Badan Pusat Statistik (2022) *Statistik Hortikultura 2022*, Jakarta: Badan Pusat Statistik.
7. Badan Pusat Statistik (2018) *The First Indonesian Agriculture Integrated Survey (AGRIS)*, Badan Pusat Statistik Kabupaten Penajam Paser Utara.
8. Wang L, Liang W, Xing J, et al. (2013) Dynamics of chloroplast proteome in salt-stressed mangrove *Kandelia candel* (L.) Druce. *J Proteome Res* 12: 5124–5136. https://doi.org/10.1021/pr4006469
9. Niinemets Ü, Valladares F (2004) Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biol* 6: 254–268. https://doi.org/10.1055/s-2004-817881
10. Niinemets Ü (2007) Photosynthesis and resource distribution through plant canopies. *Plant Cell Environ* 30: 1052–1071. https://doi.org/10.1111/j.1365-3040.2007.01683.x
11. Laanisto L, Niinemets Ü (2015) Polytolerance to abiotic stresses: how universal is the shade–drought tolerance trade-off in woody species? *Glob Ecol Biogeogr* 24: 571–580. https://doi.org/10.1111/geb.12288
12. Hillis DM, Sadava D, Heller HC, et al. (2012) Principles of life. USA: Sinauer Associates Inc.
13. Nguyen GN, Lantzke N, Van Burgel A (2022) Effects of shade nets on microclimatic conditions, growth, fruit yield, and quality of eggplant (*Solanum melongena* L.): a case study in Carnarvon, Western Australia. *Horticulturae* 8: 696. https://doi.org/10.3390/horticulturae8080696
14. Kesumawati E, Apriyatna D, Rahmawati M (2020) The effect of shading levels and varieties on the growth and yield of chili plants (*Capsicum annuum* L.). *IOP Conf Ser Earth Environ Sci* 425: 012080. https://doi.org/10.1088/1755-1315/425/1/012080
15. Baharuddin R, Chozin M, Syukur M (2014) Shade tolerance of 20 genotypes of tomato (*Lycopersicon esculentum Mill*). *Indones J Agron* 42: 130–135. https://doi.org/10.24831/jai.v42i2.8431
16. Putri DRM, Syukur M, Ritonga AW (2025) Variability of yield and yield components of 23 hybrid cayenne pepper (*Capsicum frutescens*) genotypes under shaded and unshaded conditions. *Biodiversitas J Biol Divers* 26: 396–406. https://doi.org/10.13057/biodiv/d260139
17. Sopandie D (2014) Fisiologi Adaptasi Tanaman terhadap Cekaman Abiotik pada Agroekosistem Tropika, Bogor: IPB Press.
18. Kumar A, Sharma V, Jain BT, et al. (2020) Heterosis breeding in eggplant (*Solanum melongena* L.): gains and provocations. *Plants* 9: 403. https://doi.org/10.3390/plants9030403

19. Acquaah G (2012) *Principles of Plant Genetics and Breeding*, 2 Eds., New York (NY): Wiley.
20. Mir R, Calabuig-Serna A, Seguí-Simarro JM (2021) Doubled haploids in eggplant. *Biology* 10: 685. https://doi.org/10.3390/biology10070685
21. Prigge V, Xu X, Li L, et al. (2012) New insights into the genetics of *in vivo* induction of maternal haploids, the backbone of doubled haploid technology in maize. *Genetics* 190: 781–793. https://doi.org/10.1534/genetics.111.133066
22. Tamilzharasi M, Umamaheswari D, Umabalan J, et al. (2024) Doubled haploid rice breeding. In: Singh A, Singh SK, Shrestha J (Eds.), *Climate-Smart Rice Breeding*, Singapore, Springer Nature Singapore, 63–87. https://doi.org/10.1007/978-981-97-7098-4_4
23. Boughazi K, Wuyts N, Muller O, et al. (2024) Doubled haploid lines derived from a european maize flint landrace contrast in recovery from cold stress. *Agronomy* 14: 408. https://doi.org/10.3390/agronomy14030408
24. Rivas-Sendra A, Campos-Vega M, Calabuig-Serna A, et al. (2017) Development and characterization of an eggplant (*Solanum melongena*) doubled haploid population and a doubled haploid line with high androgenic response. *Euphytica* 213: 89. https://doi.org/10.1007/s10681-017-1879-325
25. Mulyana A, Purwoko BS, Dewi IS, et al. (2023) Comparison of six anther culture methods for the production of doubled haploids in eggplant (*Solanum melongena* L.). *Euphytica* 219: 44. https://doi.org/10.1007/s10681-023-03171-8
26. Rotino GL, Acciarri N, Sunseri F Development of eggplant varietal resistance to insects and diseases via plant breeding. *Adv Hortic Sci* 11: 193–201.
27. Caguiat X, Hautea D (2014) Genetic diversity analysis of eggplant (*Solanum melongena* L.) and related wild species in the Philippines using morphological and SSR markers. *SABRAO J Breed Genet* 46: 183–201.
28. Kumar S, Arumugam T, Ulaganathan V (2016) Genetic diversity in eggplant germplasm by principal component analysis. *SABRAO J Breed Genet* 48: 167–171.
29. Niazian M, Shariatpanahi ME (2020) In vitro-based doubled haploid production: recent improvements. *Euphytica* 216: 69. https://doi.org/10.1007/s10681-020-02609-7
30. Sabra D, Younis A, Nassar S, et al. Performance of 30 maize double haploid lines under drought stress and soil conditioners. *J Chem Health Risks* 14: 1199–1211.
31. Fereidooni L, Tahmasebi Z, Kahrizi D, et al. (2023) Evaluation of drought resistance of camelina (*Camelina sativa* L.) doubled haploid lines in the climate conditions of kermanshah province. *Agrotech Ind Crops* 4: 134–146. https://10.22126/atic.2023.9570.1111
32. Al-Ashkar I, Romdhane WB, El-Said RA, et al. (2021) Agro-physiologic responses and stress-related gene expression of four doubled haploid wheat lines under salinity stress conditions. *Biology* 10: 56. https://doi.org/10.3390/biology10010056
33. Ma'arif S, Purwoko BS, Ritonga AW, et al. (2024) Study of genetic variability and shade tolerance of doubled haploid lines of eggplant (*Solanum melongena* L.) obtained from anther culture. *Bogor Agricultural University, Faculty of Agriculture,* Bogor, Indonesia, 99p.
34. Wang X, Shen L, Liu T, et al. (2022) Microclimate, yield, and income of a jujube–cotton agroforestry system in Xinjiang, China. *Ind Crops Prod* 182: 114941. http://doi.org/10.1016/j.indcrop.2022.114941

35. Yan Z, He D, Niu G, et al. (2019) Evaluation of growth and quality of hydroponic lettuce at harvest as affected by the light intensity, photoperiod and light quality at seedling stage. *Sci Hortic* 248: 138–144. https://doi.org/10.1016/j.scienta.2019.01.002
36. Fan X-X, Xu Z-G, Liu X-Y, et al. (2013) Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. *Sci Hortic* 153: 50–55. https://doi.org/10.1016/j.scienta.2013.01.017
37. Kalmatskaya OA, Karavaev VA, Tikhonov AN (2019) Induction of chlorophyll fluorescence in Tradescantia leaves acclimated to growth light of different intensities. In: Tuchin VV, Genina EA (Eds.), *Saratov Fall Meeting 2018: Optical and Nano-Technologies for Biology and Medicine*, Saratov, Russian Federation, SPIE, 72. https://doi.org/10.1117/12.2523333
38. Ding J, Zhao J, Pan T, et al. (2019) Comparative transcriptome analysis of gene expression patterns in tomato under dynamic light conditions. *Genes* 10: 662. https://doi.org.10.3390/genes10090662
39. Vialet-Chabrand S, Matthews JSA, Simkin AJ, et al. (2017) Importance of fluctuations in light on plant photosynthetic acclimation. *Plant Physiol* 173: 2163–2179.
40. Prabhu M, Natarajan S, Veeraragavathatham D (2008) Correlation and path coefficient analysis in eggplant (*Solanum melongena* L.). *Indian J Agric Res* 42: 232–234.
41. Khalid MHB, Raza MA, Yu HQ, et al. (2019) Effect of shade treatments on morphology, photosynthetic and chlorophyll fluorescence characteristics of soybeans (*Glycine max L. Merr*.). *Appl Ecol Environ Res* 17: 2551–2569. https://doi.org/10.15666/aeer/1702_25512569
42. Ma L, Li G (2019) Auxin-dependent cell elongation during the shade avoidance response. *Front Plant Sci* 10: 914. https://doi.org/10.3389/fpls.2019.00914
43. Jiang Y, Ding X, Wang J, et al. (2021) Decreased low-light regulates plant morphogenesis through the manipulation of hormone biosynthesis in *Solanum lycopersicum*. *Environ Exp Bot* 185: 104409. https://doi.org/10.1016/j.envexpbot.2021.104409
44. Frébortová J, Frébort I (2021) Biochemical and structural aspects of cytokinin biosynthesis and degradation in bacteria. *Microorganisms* 9: 1314. https://doi.org/10.3390/microorganisms9061314
45. Hussain HA, Men S, Hussain S, et al. (2019) Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. *Sci Rep* 9: 3890. https://doi.org/10.1038/s41598-019-40362-7
46. Wu Y, Gong W, Yang W (2017) Shade inhibits leaf size by controlling cell proliferation and enlargement in soybean. *Sci Rep* 7: 9259. https://doi.org/10.1038/s41598-017-10026-5
47. Zhang H, Cao Y, Wang Z, et al. (2023) Functional mapping of genes modulating plant shade avoidance using leaf traits. *Plants* 12: 608. https://doi.org/10.3390/plants12030608
48. Ren B, Zhang J, Dong S, et al. (2017) Regulations of 6-Benzyladenine (6-BA) on leaf ultrastructure and photosynthetic characteristics of waterlogged summer maize. *J Plant Growth Regul* 36: 743–754. https://doi.org/10.1007/s00344-017-9677-7
49. Ilić ZS, Fallik E (2017) Light quality manipulation improves vegetable quality at harvest and postharvest: A review. *Environ Exp Bot* 139: 79–90. https://doi.org/10.1016/j.envexpbot.2017.04.006
50. Sunaryanti D, Chozin M, Aziz S (2018) Growth analysis and physiological characteristics of several tomato genotipes under the low light intensity. *J ISSAAS* 24: 129–140.
51. Panigrahy M, Ranga A, Das J, et al. (2019) Shade tolerance in Swarnaprabha rice is associated with higher rate of panicle emergence and positively regulated by genes of ethylene and cytokinin pathway. *Sci Rep* 9: 6817. https://doi.org/10.1038/s41598-019-43096-8

52. Munir M, Jamil M, Baloch J, et al. (2004) Impact of light intensity on flowering time and plant quality of *Antirrhinum majus* L. cultivar Chimes White. *J Zhejiang Univ-Sci A* 5: 400–405. https://doi.org/10.1631/jzus.2004.0400
53. Faust JE, Holcombe V, Rajapakse NC, et al. (2005) The effect of daily light integral on bedding plant growth and flowering. *Hort Science* 40: 645–649. https://doi.org/10.21273/hortsci.40.3.645
54. Cober ER, Voldeng HD (2001) Low R:FR light quality delays flowering of *E7E7* soybean lines. *Crop Sci* 41: 1823–1826. https://doi.org/10.2135/cropsci2001.1823
55. Qin F, Shen Y, Li Z, et al. (2022) Shade delayed flowering phenology and decreased reproductive growth of *Medicago sativa* L. *Front Plant Sci* 13: 835380. https://doi.org/10.3389/fpls.2022.835380
56. Stagnari F, Ficcadenti N, Manetta AC, et al. (2022) Modulation of light and nitrogen for quality-traits improvement: a case study of altino sweet pepper. *Horticulturae* 8: 499. https://doi.org/10.3390/horticulturae8060499
57. Hope E, Carins-Murphy MR, Hudson C, et al. (2020) Opium poppy capsule growth and alkaloid production is constrained by shade during early floral development. *Ann Appl Biol* 176: 296–307. https://doi.org/10.1111/aab.12581
58. Choi HG (2021) Correlation among phenotypic parameters related to the growth and photosynthesis of strawberry (*Fragaria* × *ananassa Duch*.) grown under various light intensity conditions. *Front Plant Sci* 12: 647585. https://doi.org/10.3389/fpls.2021.647585
59. Solankey SS, Kumari M, Akhtar S, et al. (2021) Challenges and Opportunities in Vegetable Production in Changing Climate: Mitigation and Adaptation Strategies, In: Solankey SS, Kumari M, Kumar M (Eds.), *Advances in Research on Vegetable Production Under a Changing Climate*, Cham: Springer International Publishing, 13–59. https://doi.org/10.1007/978-3-030-63497-1_2
60. Leonardi C, Guichard S, Bertin N (2000) High vapour pressure deficit influences growth, transpiration and quality of tomato fruits. *Sci Hortic* 84: 285–296. https://doi.org/10.1016/s0304-4238(99)00127-2
61. Yang F, Liu Q, Cheng Y, et al. (2020) Low red/far-red ratio as a signal promotes carbon assimilation of soybean seedlings by increasing the photosynthetic capacity. *BMC Plant Biol* 20: 148. https://doi.org/10.1186/s12870-020-02352-0
62. Touil S, Richa A, Fizir M, et al. (2021) Shading effect of photovoltaic panels on horticulture crops production: A mini review. *Rev Environ Sci Biotechnol* 20: 281–296. https://doi.org/10.1007/s11157-021-09572-2
63. Laub M, Pataczek L, Feuerbacher A, et al. (2022) Contrasting yield responses at varying levels of shade suggest different suitability of crops for dual land-use systems: a meta-analysis. *Agron Sustain Dev* 42: 51. https://doi.org/10.1007/s13593-022-00783-7
64. Susanti ED, Chozin MA, Ritonga AW, et al. (2023) Identification of morpho-physiological and yield traits of sweet corn hybrids at various shade levels. *Caraka Tani J Sustain Agric* 38: 327. http://doi.org/10.20961/carakatani.v38i2.73567
65. Xie X, Cheng H, Hou C, et al. (2022) Integration of light and auxin signaling in shade plants: from mechanisms to opportunities in urban agriculture. *Int J Mol Sci* 23: 3422. http://doi.org/10.3390/ijms23073422
66. Liu W, Tollenaar M (2009) Physiological mechanisms underlying heterosis for shade tolerance in maize. *Crop Sci* 49: 1817–1826. http://doi.org/10.2135/cropsci2008.07.0423
67. Shifriss C, Pilowsky M, Aloni B (1994) Variation in flower abscission of peppers under stress shading conditions. *Euphytica* 78: 133–136. http://doi.org/10.1007/bf00021408

68. Shehata S, Elsagheer A, El-Helaly M, et al. (2013) Shading effect on vegetative and fruit characters of tomato plant. *J Appl Sci Res* 9: 1434–1437.
69. Otoni BDS, Mota WFD, Belfort GR, et al. (2012) Produção de híbridos de tomateiro cultivados sob diferentes porcentagens de sombreamento. *Rev Ceres* 59: 816–825. https://doi.org/10.1590/s0034-737x2012000600012
70. Masabni J, Sun Y, Niu G, et al. (2016) Shade effect on growth and productivity of tomato and chili pepper. *HortTechnology* 26: 344–350. https://doi.org/10.21273/HORTTECH.26.3.344
71. Siahaan GF, Muhamad Achmad Chozin, Muhamad Syukur, et al. (2022) Perbedaan respon pertumbuhan, fisiologi dan produksi 20 genotipe cabai rawit terhadap berbagai tingkat naungan. *J Agron Indones Indones J Agron* 50: 73–79. https://doi.org/10.24831/jai.v50i1.38832